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Polyandry is context dependent but not convenient in a mostly monandrous wasp

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Research over the past two decades suggests that polyandry is almost ubiquitous in nature. In some cases, females can gain direct and indirect (genetic) fitness benefits from mating with multiple males. However, when females accept superfluous matings without gaining any clear benefit, polyandry has been interpreted as a strategy to mitigate the costs of resisting or avoiding matings, a situation known as convenience polyandry. When females mate out of 'convenience' the mating rate is expected to be plastic, since females should mate at a higher rate when the costs of resistance or avoidance are high, for instance when males occur in high densities and/or around resources required by females such as oviposition sites. Here we show that remating in *Nasonia vitripennis*, a species of wasp that is largely monandrous in the wild but that evolves polyandry under laboratory culture, is dependent upon the availability of hosts for oviposition and upon male density. We found that females mated at a higher rate when male density was high but only if a suitable oviposition substrate was available. Outwardly this seems suggestive of convenience polyandry. However, females that remated under these conditions did not gain more time to oviposit than females that resisted superfluous matings. The results of this study highlight the importance of comprehensively assessing the costs and benefits of mating before attributing the observed behaviour to convenience polyandry. Furthermore, these results add to the growing body of evidence that the ecological context under which sexual interactions occur is critical to the economics of mating.

The causes and consequences of polyandry have become the subject of intensive study in recent years (Pizzari & Wedell, 2013). Hypotheses for the evolution and maintenance of polyandry consider that females gain direct material benefits and/or indirect genetic benefits from mating with multiple males. The most clear-cut examples of direct benefits occur when males provide females with nuptial gifts that females can use to augment their fecundity (Arnqvist & Nilsson, 2000). Traditionally, indirect genetic benefits have been assumed to arise through increased offspring fitness (Yasui, 1998). Other possibilities include genetic bet hedging (Watson, 1991), where polyandry is a risk-averse strategy that serves to protect against reproductive failure, for instance due to genetic incompatibility or low male quality (Greenway, Dougherty & Shuker, 2015; Tregenza & Wedell, 2000; Zeh & Zeh, 1996, 1997) or to ensure offspring genetic diversity when environmental conditions are unpredictable (Yasui, 1998).

However, females may mate multiply not to gain benefits as such, but rather to minimize the costs of resisting or avoiding unnecessary matings. When multiple mating serves to mitigate costs in this way it is known as 'convenience polyandry' (Thornhill & Alcock, 1983). Convenience polyandry has been suggested in a number of different taxa (sepsid flies Teuschl & Blanckenhorn, 2007; Teuschl, Hosken, & Blanckenhorn, 2007; coleopid flies: Blyth & Gilburn, 2006; the butterfly *Bicyclus anynana*: Janowitz & Fischer, 2012; the spider *Stegodyphus lineatus*: Maklakov & Lubin, 2004) but only in the Gerridae (pond skaters and water striders) have females been demonstrated to modify their mating rate based on the relative costs of resistance and mating (see Rowe, 1992; Rowe, Arnqvist, Sih, & Krupa, 1994; Watson, Arnqvist, & Stallmann, 1998; Wilcox, 1984).

Convenience polyandry has also been proposed as a strategy that females adopt when male density is high in order gain more uninterrupted time in which to oviposit. In the damselfly *Calopteryx haemorrhoidalis haemorrhoidalis*, for instance, Rivera and Andrés (2002) found that females with a higher mating frequency spent longer ovipositing, suggesting that accepting otherwise superfluous copulations increased oviposition opportunities. The presence of a suitable substrate on which to oviposit has also been shown to

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increase female mating rate in the seed beetles *Callosobruchus maculatus* (Fox & Hickman, 1994) and *Callosobruchus chinensis* (Harano, Fujisawa, & Miyatake, 2006). However, the presence of an oviposition substrate may also serve to elevate male harassment, as in the case of the seaweed fly *Coleopa frigida* (Meader & Gilburn, 2008). If males are present in high numbers at oviposition sites then mating may be the least costly strategy, both in terms of access to oviposition sites and in terms of reducing the costs of resisting many male mating attempts. Furthermore, females may gain more time to oviposit without interruption if males mate-guard the females with which they have copulated and by doing so protect them against further harassment.

Here we consider whether polyandry by females of the parasitoid wasp *Nasonia vitripennis* serves to mitigate the costs of harassment during oviposition. In the wild, female *N. vitripennis* rarely mate more than once (Grillenberger et al., 2008), but the proportion of females that mate multiply repeatedly evolves in laboratory culture (van den Assem & Jachmann, 1999; Burton-Chellew, Beukeboom, West, & Shuker, 2007) and there is segregating genetic variation in female mating rate (Shuker, Phillimore, Burton-Chellew, Hodge, & West, 2007). Female *N. vitripennis* are therefore 'mostly monandrous' (Boulton & Shuker, 2015a), and provide us with the opportunity to explore the origin of polyandry, albeit in a laboratory setting. Typically, behavioural ecologists interested in the evolution of polyandry have considered already polyandrous species (for sensible logistic reasons), but this does mean that much of what we know addresses the maintenance of polyandry, rather than necessarily its origin.

Female *Nasonia* allocate sex according to the predictions of local mate competition theory (LMC; Grillenberger et al., 2008; Hamilton, 1967; Werren, 1980), producing very female-biased sex ratios when ovipositing alone in order to maximize grand-offspring production. Females disperse after mating in order to find a host on which to oviposit, but the brachypterous (short-winged) males remain at the natal patch and are unable to disperse. However, under laboratory culture females oviposit on hosts in large groups, producing the more even sex ratios predicted by LMC theory (e.g. Werren, 1983). Moreover, females cannot disperse away from males when confined in a mass culture tube, as such, some males are often present after provisioning of fresh hosts on which to oviposit. Owing to these changes, both the magnitude and the temporal scale of harassment females experience is likely to differ from most situations in the wild.

Recent work has shown that exposure to males in the absence of hosts on which to oviposit does not result in a survival cost to female *N. vitripennis*, but when hosts are present female longevity is reduced in more male-biased conditions (Boulton & Shuker, 2015a). Independently of any survival cost, females maintained with multiple males also laid fewer eggs and produced sex ratios that were not representative of the high level of LMC expected to be experienced by offspring (i.e. the sex ratios were less female biased than expected: Boulton & Shuker, 2015a, 2015b). Work by van den Assem and Feuth-de-Bruijn (1977) has shown that second matings temporarily disrupt the laying of fertilized eggs (since *N. vitripennis* is haplodiploid, fertilized eggs develop as daughters and unfertilized eggs as sons). Taken together, these observations suggest that *N. vitripennis* are more likely to mate multiply when exposed to many males and hosts simultaneously. However, by doing so they suffer a cost in terms of their ability to allocate sex optimally (Boulton & Shuker, 2015b).

The aim of the current study was two-fold. First, we investigated whether female polyandry is context dependent, with females modifying their receptivity to second matings according to the level of harassment they experience and/or the presence of hosts. Second, we assessed whether any such modification represents convenience polyandry. To determine whether polyandry is context dependent, we varied the male density and host availability and observed how these changes influenced both male harassment and courtship, and how females responded to males. Based on our previous findings, we predicted that females would be more likely to remate under conditions of high harassment when hosts are present. If host presence and harassment do modify female receptivity, we predicted that they would do so in order to mitigate the costs of harassment. To test this possibility, we observed instances of oviposition and allowed females to oviposit for 24 h in their treatment conditions (high versus low harassment). If there is convenience polyandry, we would expect females that remate when resistance is more costly (when male density is high) to gain more uninterrupted time to oviposit and so lay more eggs in total.

METHODS

Study Animals

Nasonia vitripennis (Chalcidoidea: Pteromalidae) is a gregarious idiobiont parasitoid that attacks dipteran pupae (Whiting, 1967). The strain of *N. vitripennis* used for all experiments was HVRx. This line was created from five lines of wild-caught wasps collected from Hoge Veluwe national park in the Netherlands in 2001 and is maintained as a large outbred population (by mixing stock tubes containing pupae (*Calliphora vicinia*) each generation; van de Zande et al., 2014).

We harvested focal males and females from a grandparental generation of virgin and mated females respectively, in order to standardize the development of experimental individuals. Females were isolated prior to emergence and maintained alone, while we allowed males to emerge naturally and maintained them with brothers (29 male families were used and their identity was recorded).

On the day of emergence, we mated virgin females to a single male, after which each female was kept in isolation and provided with honey solution on which to feed. We recorded the family of the male with which the female initially mated, and we only exposed females to males from the same family throughout the experiment in order to standardize and reduce any possible indirect genetic benefits that females could gain from mating multiply (although no such benefits have yet been found: see Boulton & Shuker, 2015a). Experiments were carried out across three experimental blocks (1: 14–17 November 2014; 2: 28–31 November 2014; 3: 30 November–2 December 2014) and all observations were conducted between 0900 and 1400 hours.

Observations

Twenty-four hours after the first mating we tested whether the number of males present or the availability of hosts influenced male harassment, courtship and female remating using a factorial design. Females were observed for 20 min in the following conditions: (1) alone, no hosts, $N = 26$; (2) low harassment (one male), no hosts, $N = 26$; (3) high harassment (three males), no hosts, $N = 26$; (4) alone, one host available, $N = 27$; (5) low harassment, one host available, $N = 26$; (6) high harassment, one host available, $N = 26$ (total $N = 157$ females). We did not perform behavioural observations on females in treatment (1), but maintained them to test their remating rate after 48 h (see below).

Over the 20 min observation period, we conducted scan samples every 30 s, and for each scan we recorded whether the female was being harassed or courted by one or several males, was copulating and whether she was commencing oviposition (by drilling into the host; it is unlikely that many eggs would themselves be laid within

20 min, although we use the term oviposition for simplicity: see Whiting, 1967). Harassment was recorded whenever a male was in contact with or attempting to contact a female, but was not in the stereotypical courtship posture. Courtship was recorded whenever a single male adopted the stereotypical courtship posture first described by van den Assem and Visser (1976). Briefly, *N. vitripennis* males chase and mount females, and once mounted the male will perform a series of 'head-nod' behaviours, which coincide with the release of a pheromone from the mouthparts. A receptive female will then open her genital pore and lower her antenna and the male will back up and copulate. After the male has finishing copulating, he will resume courtship, and this postcopulatory courtship serves to reduce female receptivity to future matings. If the female does not signal receptivity the male will eventually dismount and move away. Mass courtship was recorded whenever multiple males were mounted on the female. For any copulations that took place we recorded the time at which they occurred. This allowed behavioural differences before and after copulation to be determined.

Postobservation Period

After the initial 20 min observation period, we removed hosts (if present: treatments 4–6) and replaced them with six fresh hosts. We maintained the females in their treatment conditions for 24 h at 25 °C, after which all males and hosts were removed and all females were again provided with honey solution. Where females were given hosts (treatments 4–6), these were maintained at 25 °C. After the offspring had died they were counted in order to assess the influence of harassment and remating on fecundity and sex allocation.

Finally, to test whether a female's previous experience of hosts and harassment influenced her remating rate, we exposed all females to an additional male after a further 24 h in isolation (48 h after the initial observation period) and recorded whether or not the female became receptive after the male initiated courtship.

Statistical Analysis

We analysed the effect of male density and host presence (as well as the interaction effect) on the frequency of harassment and courtship (calculated as the total number of bouts of harassment/courtship recorded during the 20 min observation trial) using two-way ANOVA in R (version 3.1.2, The R Foundation for Statistical Computing, Vienna, Austria, http://www.r-project.org). This analysis considered treatments 2–3 and 5–6 (i.e. where males were present). We analysed whether treatment influenced the remating rate using general linear models with a binomial error structure and a logit link function in R (package lme4). We also included male family identity in these models in order to test whether males from different families varied in their tendency to harass and court females, and whether or not males from certain families were more successful at achieving second matings (if this was found to be the case, male family was included as a random effect in models testing the main treatment effects). We tested whether females that did remate varied in how many courtship bouts they experienced before they became receptive using a zero-inflated model (many females mated on the first attempt, which was scored as zero).

One way in which polyandry may be convenient is if females experience reduced harassment after copulating. We tested whether females experienced a change in harassment or courtship rate before and after mating (and any interaction with treatment) using a mixed model in R with female identity as a random effect. Females that mated in the first or last 30 s were excluded from this analysis, as this limited the opportunity for events to occur before or after mating, respectively.

We tested whether male density or female remating had any influence on offspring production of females in treatments 4–6 using a using two-way ANOVA. We also tested whether females that remated produced less female-biased sex ratios using glms with a binomial error structure and a logit link function in R. All models included experimental block as a random effect.

Ethical Note

This research adheres to the guidelines set out by ASAB as well as ethical codes of practice implemented by the University of St Andrews. The experimental procedures implemented here were not invasive and involved only observations of behaviour and offspring production. The sample sizes reported were considered appropriate to maximize statistical power while reducing the number of individuals involved in the experiments.

RESULTS

Harassment

Females that were maintained with three males experienced more harassment ($F_{1,98} = 43.17$, $P < 0.0001$; Fig. 1a) than those maintained with a single male. There was no effect of host presence alone on harassment ($F_{1,98} = 3.19$, $P = 0.08$) but there was a significant interaction effect between male number and host presence. This is driven by the fact that the presence of a host reduced the amount of harassment a female experienced when a single male was present, but not when there were three males (interaction: $F_{1,98} = 1.77$, $P = 0.03$; see Fig. 1a). Additionally, male family was significantly associated with variation in harassment ($F_{29,98} = 1.71$, $P = 0.04$).

Courtship

There was no effect of the number of males ($F_{1,98} = 0.21$, $P = 0.65$) or the presence of hosts ($F_{1,98} = 0.27$, $P = 0.60$) on the time a female spent in courtship. Females in the multimale treatments (3 and 6) were frequently engaged by two or more courting males at once (i.e. mass courtships). If mass courtship is included in this analysis, females in the three-male treatments then did indeed experience more courtship events ($F_{1,98} = 31.16$, $P < 0.0001$; Fig. 1b) but host presence still did not influence courtship frequency ($F_{1,98} = 0.42$, $P = 0.52$) nor was there an interaction between host presence and number of males in terms of courtship ($F_{1,98} = 2.66$, $P = 0.11$). Again, male family significantly affected the number of courtships a female experienced ($F_{29,98} = 2.20$, $P < 0.005$).

Remating Propensity

Females were more likely to remate during the first 20 min mating trial when multiple males were present (binomial: LRT = 5.52, $df = 1$, $P = 0.018$) but host presence alone had no effect on female remating behaviour (LRT = 0.001, $df = 1$, $P = 0.97$). Importantly, there was a significant interaction between male number and host presence (LRT = 6.61, $df = 1$, $P = 0.013$; Fig. 1c). When hosts were present, females in the presence of three males remated approximately two-thirds of the time, but without hosts the effect of one versus three males was negligible. The lowest remating rate was for females kept with one male, with hosts. Although male families appeared to differ in their tendency to court

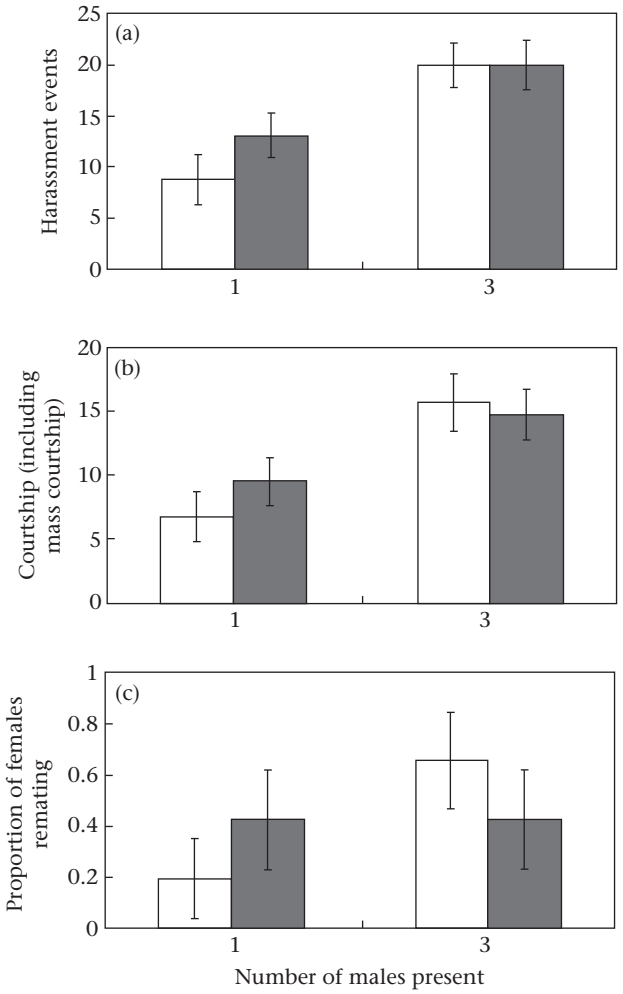

Figure 1. Influence of male density and host presence on (a) the number of harassment events experienced by females, (b) the number of courtship events (including mass courtships, see text for details) experienced by females and (c) female tendency to remate. Error bars = 95% confidence intervals. For (c) confidence intervals were calculated using the Wald method. Unshaded bars: hosts available; shaded bars: hosts unavailable.

and harass females, there was no significant effect of male family ID on female remating (LRT = 41.08, $df = 29$, $P = 0.07$).

Remating Latency

Females that were maintained with both three males and hosts took more courtships to become receptive (zero-inflated model, interaction between male number and host presence: LRT = 6.56, $df = 1$, $P < 0.01$; Fig. 2). However, neither the number of males (LRT = 0.11, $df = 1$, $P = 0.74$) nor host presence (LRT = 2.86, $df = 1$, $P = 0.09$) was significant as a main effect.

Courtship and Harassment after Mating

Females that accepted a second mating experienced a lower rate of courtship after copulation than before (LRT = 23.40, $df = 1$, $P < 0.0001$), regardless of the number of males present (LRT = 1.37, $df = 1$, $P = 0.24$). However, females were found to experience more harassment after mating than before (LRT = 14.97, $df = 1$, $P < 0.0005$), which occurred regardless of the number of males present (LRT = 0.42, $df = 1$, $P = 0.51$; Fig. 3).

Host-directed Behaviour and Offspring Production

In treatments in which hosts were available, male presence was costly to females in terms of reducing the amount of time females spent on hosts (quasi-Poisson LRT = 16.06, $df = 2$, $P < 0.001$) and the time spent drilling into hosts and commencing oviposition (zero-inflated Poisson: LRT = 48.14, $df = 2$, $P < 0.0001$). Regardless of the number of males present, females that remated engaged in fewer bouts of oviposition (zero-inflated Poisson: LRT = 6.76, $df = 2$, $P = 0.034$) but sample sizes were insufficient to test whether there was any interaction with male number (only one female in the three-male treatment was observed to begin oviposition). Across 24 h, females exposed to one or three males laid a similar number of eggs to those allowed to oviposit alone ($F_{2,68} = 0.16$, $P = 0.85$; only females exposed to one or three males: $F_{1,45} = 0.43$, $P = 0.51$). When we considered females that had the opportunity to remate, there was also no association between remating and fecundity ($F_{1,45} = 2.51$, $P = 0.12$) nor any interaction between male number and remating ($F_{1,45} = 0.22$, $P = 0.64$).

The sex ratio of clutches produced by females that experienced more harassment were closer to equality (quasibinomial: $F_{2,67} = 3.59$, $P = 0.033$). Females observed to remate also produced more equal sex ratios ($F_{2,67} = 5.44$, $P = 0.006$; Fig. 4), and these effects were independent of each other (interaction: $F_{1,67} = 2.83$, $P = 0.10$). When females that did not have an opportunity to mate (treatments 1 and 4) were excluded, the effect of remating ($F_{1,46} = 4.77$, $P = 0.034$) and the interaction effect ($F_{1,46} = 2.26$, $P = 0.14$) were consistent but the significant effect of male number disappeared ($F_{1,46} = 1.95$, $P = 0.17$).

Remating after 24 h

Remating rates after a further 24 h were very low, only 14.75% of females (18 of 122) being receptive during this final trial. Perhaps unsurprisingly, therefore, there was no effect of previous experience of male number or host availability on remating (binomial LRT = 0.000, $df = 1$, $P = 0.99$ and LRT = 0.002, $df = 1$, $P = 0.96$, respectively). The interaction was also not significant (LRT = 0.12, $df = 1$, $P = 0.72$). Furthermore, females that remated previously were no more or less likely to remate 24 h later than those that had earlier resisted (LRT = 2.35, $df = 1$, $P = 0.12$).

DISCUSSION

Polyandry in the mostly monandrous *N. vitripennis* is context dependent, varying with the number of males present and the presence or absence of hosts. Moreover, these effects are transient, with female remating rate dropping after a further period of isolation. Females were more likely to accept a second mating when male density was higher and when hosts were available. When male density was low, however, females were more likely to remate when hosts were absent. When more males were present, females did experience more harassment and courtship, but in the presence of only a single male, the availability of a host appeared to protect females from harassment in some way. Females in this treatment experienced fewer mating opportunities (i.e. fewer courtships), which was consistent with the lower remating rate (19%). In this case, increasing the complexity of the environment by introducing hosts perhaps helped females to evade searching males. However, the presence of hosts did not appear to help when three males were searching, and in this condition females were unlikely to remain undiscovered.

Superficially, our findings are suggestive of convenience polyandry, particularly when we also consider female latency to remate. Females that were receptive to second matings signalled their

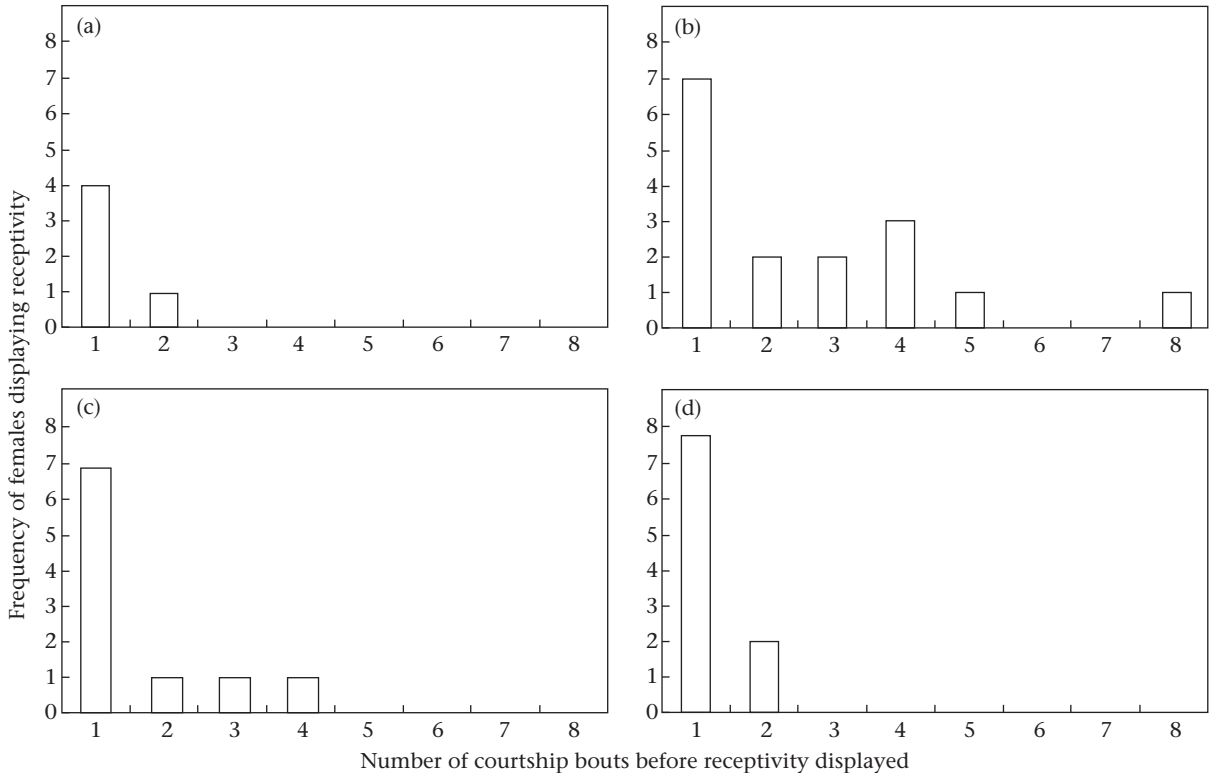

Figure 2. Number of courtships experienced by females before they displayed receptivity according to male density and host presence. (a) One male, with hosts, (b) three males with hosts, (c) one male, no hosts and (d) three males, no hosts.

willingness to mate on average after 1.3 attempted matings. When we consider females in the treatment group that exhibited the highest remating rate (those that were maintained with three males and hosts) females typically experienced twice the number of mating attempts before becoming receptive. One possible interpretation for this pattern is that as the level of polyandry increases across the treatments, so the number of females accepting rematings that are otherwise genetically predisposed to remain monandrous will also increase (remating rate is heritable: see Shuker et al., 2007). If these unwilling females take longer to remate, then a positive correlation between remating rate and latency to remate will emerge. Put another way, as polyandry increases, so we necessarily sample more females that have greater latencies to remate.

Under convenience polyandry, females should reduce their reluctance to mate according to the costs of harassment that will be elevated when male density is high and when male and female interests are more conflicting, for instance when females want to oviposit. Our results follow this pattern, as outlined above. However, convenience polyandry also requires that this change in female behaviour leads to cost mitigation. Here our results do not unequivocally support a convenience polyandry interpretation. First, although polyandrous females did experience fewer courtship attempts after remating, they also experienced more harassment postmating, and were less able to commence oviposition behaviours. This may occur because female *Nasonia* are less likely to permit courtship for 24 h or more after mating (e.g. Ruther, Stahl, Steiner, Garbe, & Tolasch, 2007), but males can still harass females. Second, when females oviposit soon after remating they

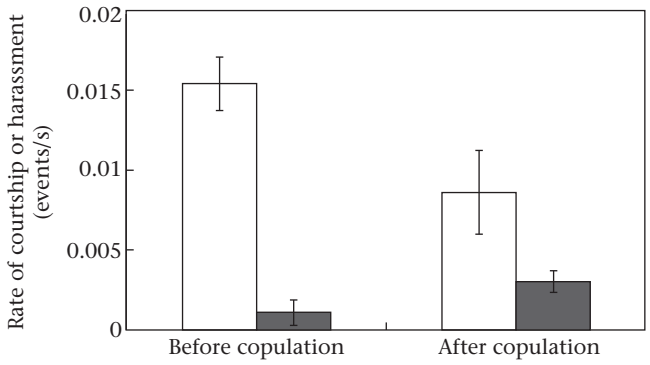

Figure 3. Harassment and courtship rate experienced by females of *Nasonia vitripennis* before and after copulating a second time (error bars = 95% confidence intervals). Shaded bars: harassment events; unshaded bars: courtship experienced by females.

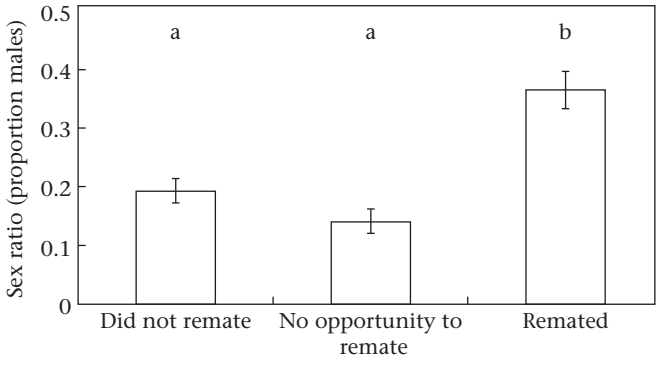

Figure 4. The influence of remating on the sex ratio produced by *Nasonia vitripennis* females. Error bars = binomial confidence intervals; lowercase letters represent groups that differ significantly ($P < 0.01$).

experience a sex allocation cost by being constrained in some way in their ability to utilize sperm fully and to produce the female-biased sex ratios expected under LMC (van den Assem & Feuth-de-Bruijn, 1977; Boulton & Shuker, 2015a, 2015b). As such, allowing themselves to be mated close to oviposition resources (i.e. in the presence of hosts) reduces a female's ability to optimally allocate sex. Third, although we also saw that males from certain families varied in their tendency to harass and court females, there was no evidence that males from high harassment families were more likely to overcome female resistance, suggesting that females were not responding to the costs of resistance imposed by individual males. In passing though, we note that our results are suggestive of genetic variation in male harassment behaviour in *N. vitripennis*, which in turn suggests that male harassment could coevolve with female resistance behaviour (i.e. Rowe & Arnqvist, 2002). Fourth, there was no evidence that females respond to the costs of harassment experienced in the past, as a female's previous experience of the operational sex ratio did not influence her propensity to remate 24 h after the end of the experiment. This contrasts with the study of Vepsalainen and Savolainen (1995), which found that in the water strider *Gerris lacustris*, females that had experienced a male-biased operational sex ratio were less reluctant to mate when tested later, suggesting that they modify their re-mating rate according to their past experience of the costs of resistance.

Finally, the fifth line of evidence questioning a convenience polyandry interpretation comes from our previous work which shows that prolonged exposure to males when oviposition resources (hosts) are present, results in females suffering reduced fecundity (Boulton & Shuker, 2015a). That experiment explored female fecundity across 10 days. Our current experiment only allowed females 24 h to oviposit, and here we have seen no costs or benefits of being kept alone or with one or three males. The 24 h period over which the current study was conducted may be insufficient for such costs of harassment to be detected. Nevertheless, our findings suggest that increased remating is unlikely to outweigh the costs of male exposure. As such, cost mitigation is unlikely to underlie the context-dependent remating that females exhibited in the presence of three males and hosts.

Although the possibility that females modify their mating rate according to the environmental and social context has typically been studied in terms of cost mitigation, i.e. convenience polyandry, there is mounting evidence to suggest that benefits-led polyandry may also be strongly dependent on both the environment and the female's own state. For instance, if females gain direct benefits from mating, then these benefits may result in higher net fitness for females in poor condition. In the spider *Pisaura mirabilis* and in the seed beetle *C. maculatus* mating carries a net benefit to females in poor condition as during mating males contribute nutrients and water, respectively (Fox, 1993; Toft & Albo, 2015). For females in good condition, however, the costs of mating are more important than the material benefits and result in a net cost of polyandry, as those females that do not require nourishment accept fewer matings. The opposite has also been found, that is, the mating rate for females in good condition is higher (the butterfly *B. anynana*: Janowitz & Fischer, 2012; the two-spot ladybird, *Adalia bipunctata*: Perry, Sharpe, & Rowe, 2009; the mouse lemur, *Microcebus muriunus* Huchard et al., 2012), perhaps because more fecund females require more sperm to ensure maximum fertility or because such females are more able to bear the costs of mating and gain genetic benefits.

The environment a female finds herself in may also shape the benefits of polyandry. For instance, in *C. maculatus* there is evidence to suggest that polyandry immediately increases the oviposition rate and stimulates oocyte maturation (Tseng, Yang, Lin, & Horng, 2007). Females may maximize the benefits they gain from remating if they do so when they have the opportunity to oviposit, i.e. in the presence of oviposition substrate. In *N. vitripennis*, it is less clear what context-dependent benefits of polyandry might accrue to females that explain why they modify their remating rate according to host presence and male density. Any such benefit would also need to overcome sex allocation costs of polyandry that arise repeatedly across our experiments (Boulton & Shuker, 2015a, 2015b; this study). To date, the only context-dependent potential benefit we have uncovered relates to male mating status, as female *N. vitripennis* increase their fecundity by mating with virgin males (Boulton & Shuker, 2015a). We are currently exploring the extent to which access to virgin males may shape the evolution of polyandry in the laboratory.

Convenience polyandry is often treated as the null hypothesis when females mate multiply without obvious benefits, or mate in a context-dependent manner. Here we have shown that although females of *N. vitripennis* modify their mating rate according to the level of harassment they experience and the presence of suitable hosts on which to oviposit, this does not appear to be a cost mitigation strategy, as remating does not reduce harassment or increase time for oviposition. These findings emphasize the problems associated with assuming that convenience polyandry is the default explanation when the female mating rate departs from what appears optimal and confirms the importance of assessing convenience polyandry more comprehensively. Our findings also add to the mounting evidence that the ecological context under which sexual interactions occur is critical when we consider the economics of mating (Cordero & Eberhard, 2003) and may fundamentally alter how we evaluate mating systems and subsequently patterns of sexual selection and sexual conflict.

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